Incorporating habitat availability into systematic planning for restoration: a species specific approach for Atlantic Forest mammals

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ABSTRACT

Aim Species persistence often depends not only on habitat protection, but also on habitat restoration. The effectiveness of species conservation through habitat restoration can be enhanced by explicitly considering "habitat availability", the combined effects of the total amount of habitat and its spatial configuration. We develop an approach for prioritizing land for restoration in a complex biome, considering habitat availability, land acquisition cost, and biogeographical representation.

Location Brazilian Atlantic Forest.

Methods We evaluate alternative restoration prioritization strategies for two mammal species with widely different dispersal abilities and habitat patch requirements. Our strategies focused on minimizing cost while meeting targets for biogeographical sub-region representation and habitat availability metrics. We evaluated solutions based on the expected post-restoration improvement in habitat availability per unit cost.

Results Restoration through land acquisition to improve habitat availability for both species and to ensure 20% forest cover within each of the Atlantic Forest biogeographical sub-regions would cost US$ 17.5-20.5 billion. The 12.6 and 11.4 million ha of restored forest resulted in an increase of 10.5% and 9.8% in habitat area and 5,518% (55-fold) and 4,100% (41-fold) in future habitat availability for *Leopardus pardalis* and *Caluromys philander*, respectively. We found a high degree of concordance (>75%) among selected planning units for each species.

Main conclusion Substantial improvements in habitat availability that benefit both species can be realized for minimal additional cost relative to solutions based solely on cost-minimization and biogeographical sub-region representation. We demonstrate that metrics based on metapopulation theory can be quantified in complex systems and used in a systematic restoration prioritization approach to improve habitat availability cost-effectively. Concordance among priority areas for restoration for species with widely different dispersal abilities and habitat patch requirements supports the idea that many species in the Brazilian Atlantic Forest might benefit from plans based on indicator species. This is particularly useful in data deficient systems like the Brazilian Atlantic Forest.

Keywords GIS, Mathematical optimization, Metapopulation, Landscape Ecology, Probability of Connectivity, Systematic Conservation Planning.

(A) INTRODUCTION

Many habitats have been severely degraded or destroyed by human activity (e.g. land clearing, fragmentation). As a result, the persistence and representation of many species will depend not only on habitat protection, but also on habitat restoration (MEA, 2005; Bowen *et al.*, 2007). Ecological restoration, the process of facilitating recovery of ecosystems following disturbance (SER, 2004), is increasingly employed as a conservation strategy worldwide (Menz *et al.*, 2013; Shackelford *et al.*, 2013).

The restored patches should meet two broad conservation objectives – representativeness and persistence (Noss *et al.*, 2009). The first objective attempts to represent the variety of populations, species or ecosystem functions of each region, while the second attempts to promote the long-term persistence of these elements (Margules & Pressey, 2000). To meet both objectives, the value of the restored habitat to the species that use it depends not only on the size of patch restored, but also on its spatial relationship with other patches in the landscape (i.e. connectivity) (Hanski & Ovaskainen, 2000; Rey Benayas *et al.*, 2009; Birch *et al.*, 2010; Menz *et al.*, 2013). Systematic conservation planning is an objective, transparent and efficient methodology for quantifying conservation value, setting explicit targets to prioritize actions among a set of sites, and provides the foundations to meet these objectives (Ball & Possingham, 2000; Margules & Pressey, 2000; Noss *et al.*, 2009).

Most previous systematic plans for restoration account for connectivity using simple neighbour metrics among planning units (Crossman & Bryan, 2006; Westphal *et al.*, 2007; Drechsler *et al.*, 2009; Thomson *et al.*, 2009; Wilson *et al.*, 2011). But the importance of connectivity from a restoration perspective relates closely to how it affects metapopulation dynamics in the long-term (Noss *et al.*, 2009). It is possible to base prioritization explicitly on models of metapopulation dynamics (e.g. Westphal *et al.*, 2003) though the methods used to solve these problems, such as stochastic dynamic programming, are infeasible for even moderately sized problems (tens to hundreds of patches; Crossman & Bryan, 2006). Ideally, in lieu of such an approach restoration prioritization should consider the ecological processes required to ensure the return of flora/fauna to the degraded sites (dispersal), while also considering representation and persistence of species of conservation concern at broad scales (complex systems with many thousands of patches).

The effectiveness of species conservation through restoration can be enhanced by explicitly considering "habitat availability", the combined effects of the total amount and quality of habitat and its spatial relationship with other patches in the landscape. Patch area (and quality) influences population viability within habitat patches (Nicholson & Possingham, 2007) while spatial configuration of patches drive patterns of dispersal success, thereby playing a key role in population supplementation and re-colonization of potential habitat patches (Hanski & Ovaskainen, 2000; Bélisle, 2005). Formal metapopulation models can require considerable data to parameterize (e.g. Hanski & Ovaskainen, 2000), making them difficult to employ in data deficient systems. Several metrics related to metapopulation theory exist, such as the "Probability of Connectivity" (*PC*; Saura & Pascual-Hortal, 2007; Appendix S1), which quantify key aspects of habitat availability but require less information and are feasible to calculate in complex problems (Saura & Rubio, 2010). The purpose of incorporating habitat availability metrics into systematic conservation planning is to provide a mechanism for explicitly accounting for the effect of habitat configuration on populations, and hence the conservation value of habitat above and beyond the benefit of area alone.

The Brazilian Atlantic Forest (hereafter BAF) is one of the world's most threatened biodiversity hotspots (Myer *et al.*, 2000), covering only 12-16% of its original 150 million ha and is in urgent need of restoration (Ribeiro *et al.*, 2009). The BAF is severely fragmented with more than 260,000 forest remnants separated by an average distance of 1,440 m from their closest neighbor (Ribeiro *et al.*, 2009). More than 80% of those remnants are smaller than 50 ha (Ribeiro *et al.*, 2009) and approximately 90% of the forest remnants are privately owned (Tabarelli *et al.*, 2005). The Atlantic Forest Restoration Pact is an agreement between more than 160 organizations and private corporations to invest US$ 77 billion to restore 15 million ha of degraded land by 2050 (www.pactomataatlantica.org.br). Successfully fulfilling this agreement would increase the amount of forest by more than 20% of its original extent. Studies by Martensen *et al.* (2008), Metzger *et al.* (2009) and Banks-Leite *et al.* (2014) have shown that landscapes with less than 20-30% of forest cover tend to hold depleted faunal communities in the BAF. Thus, the Atlantic Forest Restoration Pact could provide the minimum amount of forest cover needed to facilitate biological conservation in this biome.

Here, we develop a restoration prioritization approach that incorporates habitat availability into systematic conservation planning in a way that considers biogeographical sub-region representation and cost-effectiveness analysis. We contrasted alternative restoration priorities for two mammal species representing opposite ends of the spectrum of dispersal abilities and habitat patch requirements, and quantified the similarity of the most cost-effective solutions for each to assess how relevant the solutions might be to a wider range of species. Our key findings are that 1) explicitly considering spatial configuration of habitat in restoration prioritizations resulted in substantial improvement to habitat availability; 2) these improvements were realized for minimal additional cost relative to solutions based solely on cost-minimization and biogeographical sub-region representation, thus were cost-effective solutions; and 3) there was a high degree of concordance in priority areas for restoration for two species with widely different dispersal abilities and habitat patch requirements, suggesting such solutions may benefit a wide range of other species in the BAF. This study demonstrates the benefits of incorporating habitat availability measure into restoration prioritization problems.

(A) METHODS

In this study, we contrast alternative restoration priorities in an extensive and complex biome by undertaking five main steps (Fig. 1): 1) obtain species life history and habitat distribution data; 2) quantify current habitat availability and the individual habitat patch contribution; 3) divide the study area into planning units and quantify habitat availability metrics within each planning unit; 4) prioritize planning units for restoration under alternative restoration prioritizations; 5) simulate restoration of the priority planning units to achieve the specified target of forest cover and then quantify post-restoration habitat availability for each solution. The cost-effectiveness of each alternative restoration solution was calculated as the improvement of habitat availability per unit cost for species.

The goal of our approach is to identify planning units that, if restored, would cost-effectively improve population dynamics in this fragmented biome while also preserving any broad-scale genetic and phenotypic diversity that may exist. We use habitat availability, which accounts for both habitat area and configuration (Appendix S1), to quantify the former and biogeographical sub-region representation targets to achieve the latter. Both of these measures can be applied to systems for which detailed data on species distribution, abundance and genetic diversity is lacking, as is the case for the BAF.

(B) Step 1. Study area and species data

The BAF is located along the southeastern coast of Brazil and falls within seven main biogeographical sub-regions (Silva & Casteleti, 2003) (Fig. 2). Each biogeographical sub-region is characterised by different amounts and types of forest cover and degrees of habitat fragmentation (Ribeiro *et al.*, 2009). The Brejos Nordestinos sub-region represents less than 1% of the BAF (Ribeiro *et al.*, 2009) and was excluded from this analysis.

Although the BAF is a highly biodiverse biome, with over 2,200 vertebrate species described (Oliveira *et al.*, 2010), mammals can be considered useful surrogates to guide restoration initiatives (Wright, 2003) in data deficient systems. We chose two mammal species, the bare-tailed wooly opossum (*Caluromys philander*) and the ocelot (*Leopardus pardalis*), based on three criteria: i) terrestrial and primarily forest dwelling, ii) widely distributed in the BAF, and iii) representing low and high dispersal abilities and habitat patch requirements respectively (i.e. opposite ends of these spectrums). *C. philander* has a mean inter-habitat matrix dispersal distance of approximately 30 m, and has a mean home range size of 3 ha (Pires *et al.*, 2002), while *L. pardalis* has a mean dispersal distance of approximately 13,000 m, and has a mean home range size of 500 ha (see Appendix S2). For each species, we only considered forest remnants larger than the mean species home range (either 3 or 500 ha) as potential habitat patches.

We assume that if there is high concordance between prioritizations for these two species then the solution is also likely to benefit other species with more intermediate habitat patch requirements and dispersal abilities. Designing a solution based on an "average" species could result in solutions that are not well suited to the full range of species. Our approach is inspired by "robust" or "worst-case scenario" optimization techniques in which the most pessimistic estimates of parameters are used to identify solutions that have a high chance of avoiding poor outcomes in the face of parameter variation and uncertainty (Chinneck & Ramadan, 2000).

Forest cover was based on the BAF remnant data constructed by visual interpretation of TM/Landsat-5, ETM+/7 and CCD/CBERS-2 images, at a scale of 1:50,000, delimiting more than 260,000 forest remnants >3 ha (SOS Mata Atlântica & INPE, 2011). We used IUCN species range datasets (www.iucnredlist.org/technical-documents/spatial-data) to identify all BAF remnants falling within the species range (forest remnant maps) and meeting the minimum habitat patch requirements for each species (3 or 500 ha; habitat patch maps). These maps form the basis of our prioritization methodology.

(B) Step 2. Quantify current habitat availability and the individual habitat patch contribution

We quantified the current habitat availability within the BAF using the "Probability of Connectivity index" (*PC*) (Saura & Pascual-Hortal, 2007). *PC* quantifies the amount of habitat available to species based on a patch attribute (e.g. patch size or quality), and on a dispersal-related connectivity measure within the network of patches (Saura & Pascual-Hortal, 2007). We used habitat patch size as the patch attribute and shortest Euclidean distance between two patch boundaries as the distance attribute to calculate *PC*. We assume that the probability of direct dispersal (q_{ij}) between two patches i and j is:

$$q_{ij} = \exp(-\beta\, d_{ij}) \qquad (1)$$

where d_{ij} is the distance between patches i and j, and $1/\beta$ is the mean dispersal distance of the species. The *PC* metric is then calculated as:

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i\, a_j\, p_{ij}^{*}}{A_L^2} \qquad (2)$$

where n is the total number of patches, a_i and a_j are the patch attributes, p_{ij}^{*} is the maximum product probability of all possible paths between i and j, and A_L^2 is the square of the study area (Saura & Rubio, 2010). The probability of connection between two patches depends on the dispersal ability of the species and the presence of intermediate patches facilitating movement. The probability of a path from one patch to another is the product of dispersal probabilities (q_{ij} in eq. 1) for all connections between these two patches. The maximum product probability of connectivity is the path with highest connection probability among all possibilities between two patches. PC index varies from 0 (no habitat available) to 1 (maximum habitat availability). See Appendix S2 for further detail on how we calculated a modified version of PC index.

We also calculated the individual habitat patch contribution for the current habitat availability (ΔPC) by using an individual habitat removal experiment (Saura & Pascual-Hortal, 2007):

$$\Delta PC_k = PC - PC_{remove,k} \qquad (3)$$

where ΔPC_k is the contribution of patch k, PC is the current habitat availability value for all patches in the study area, and $PC_{remove,\,k}$ is the value after removal of patch k.

(B) Step 3. Divide study area into planning units and quantify habitat availability metrics within each planning unit

We divided the BAF into 71,871 planning units of 2,000 ha, consistent with previous studies (e.g. Pires *et al.*, 2002). For each planning unit we calculated the sum of the individual habitat patch contributions to the current habitat availability ($sum\Delta PC$). The habitat patch contribution was proportional to the area of the patch falling within the planning unit (an area-weighted sum). Thus, $sum\Delta PC$ synthesises information on the value of the habitat patches within it. Planning units that contain no habitat patches have a value of 0.

However, planning units may contain forest remnants smaller than the minimum habitat patch requirements for each species and still be valuable landscapes for restoration, especially if they are in close proximity to other forest remnants. We quantified the value of these forest remnants using a "Distance-Weighted Area" (DWA) metric that is calculated as follows:

$$DWA_i = \sum_j^n \mathrm{a}_j \exp(-\beta\, d_{ij}) \qquad (4)$$

where a_j is the forest remnant size, and $\exp(-\beta\, d_{ij})$ is the probability of direct connection between patch j and the centre of a planning unit i (similar to q_{ij} in eq. 1). Thus, DWA increases as the number and size of forest remnants contained by or near the planning unit increases (see Appendix S2 for further detail). Planning units that contain no forest remnant can have a *DWA* value greater than zero.

(B) Step 4. Prioritize planning units for restoration

We used the conservation planning software Marxan (Ball & Possingham, 2000) to identify priority planning units for restoration that meet the achievement of specific targets while minimizing cost. Marxan uses a heuristic algorithm, simulated annealing, to find solutions to the mathematical problem:

$$\text{minimize } \sum_{i=1}^{m} c_i x_i \tag{5}$$

subject to the constraint that all the representation targets are met:

$$\sum_{i=1}^{m} a_{ij} x_i \geq t_j \forall j \tag{6}$$

where *m* is the total number of planning units, c_i is the cost of restoring planning unit i, x_i is the binary decision variable indicating whether planning unit i is selected ($x_i = 1$) or not ($x_i = 0$), and a_{ij} is the contribution of planning unit i to target j. Although there are potentially many different costs associated with restoration we considered only land acquisition cost, estimated for different types of land-use within counties from the 2012 yearbook of the purchase price of rural land (see Appendix S2).

We contrasted four alternative restoration prioritization strategies for each species (with 100 Marxan runs). Two targets were common to all four strategies. The first shared target ensured that a specified total amount of forest was restored (11.4 and 12.5 million ha of forest for *C. philander* and *L. pardalis* respectively), which was based on the proportion of BAF covered by each species' range multiplied by the 15 million ha forest restoration target specified by the Atlantic Forest Restoration Pact (Table S1). The second shared target was the representation of at least 20% of each biogeographical sub-region (Table S1). This target was designed to ensure complementarity of forest types (represented by our biogeographical sub-regions) and was based on studies suggesting 20% is the minimum amount of forest required to facilitate biological conservation (Martensen *et al.*, 2008; Metzger *et al.*, 2009). Serra do Mar sub-region has >30% of forest cover and was consequently not considered for restoration (Table S1). One of the four restoration prioritization strategies was based on only these two targets. The other three strategies implemented a third target designed to improve habitat availability, based on either DWA, $sum\Delta PC$ or the additive combination of DWA and $sum\Delta PC$ ($DWA\&sum\Delta PC$). To specify these targets we ranked the planning units available for restoration (those with <60% forest cover; see below) in decreasing order of the value of the metric and then cumulatively summed these values until the specified total amount of forest was restored (first target). Thus, the values used as targets represent the theoretical maximum value achievable for a given amount of forest restored if cost constrains were not considered._We evaluated the success of all four strategies by calculating future (post-restoration) habitat availability from solutions arising from each strategy.

Only planning units with less than 60% forest cover were considered for restoration because this value represents the approximate percolation threshold (Stauffer, 1985), above which the habitat becomes highly or completely connected. No further investment in restoration is required above this threshold (Crouzeilles *et al.*, 2014), thus selected planning units were restored to 60% forest cover. There is a diminishing return on investment to restore additional habitat when this is unlikely to further increase connectivity (Pardini *et al.*, 2010). Furthermore, this is a multi-use landscape and restoration plans that exclude other land-uses entirely are unrealistic. Thus, restoring to a 60% level is a more feasible goal than trying to restore an entire planning unit within a private ownership landscape.

(B) Step 5. Simulate restoration and re-quantify habitat availability

To quantify future habitat availability, we simulated restoration resulting in 60% forest cover within the selected planning units. Areas within planning units that were never forest (e.g. sand dunes and water bodies) were not included as potential areas for restoration. The configuration of restoration within selected planning units was based on that of existing planning units containing between 59 to 61% of forest cover (n=128), which represent realistic landscape configurations (see Appendix S2 for further details). Future habitat availability was the value of *PC* based on this post-restoration simulated BAF. Simulating a landscape with restored habitat allowed us to quantify which strategy provided the greatest improvement in habitat availability relative to current habitat availability. We then calculated cost-effectiveness as the improvement in habitat availability divided by total land acquisition cost. To quantify the differences in configuration between alternative restoration priorities focused on species with widely different dispersal abilities and habitat patch requirements, we calculated the percentage of overlapping priority areas for restoration between the most cost-effective solution for each species. All analyses were carried out in R 2.12 (R Development Core Team, 2010), ArcGIS 9.3 (ESRI, 2008) and Geospatial Modelling Environment version 0.7.2.1 (Beyer, 2012).

(A) RESULTS

Large gains can be made in improving habitat availability for *C. philander* and *L. pardalis* with the Atlantic Forest Restoration Pact. The current habitat availability (*PC*) is 4.0×10^{-5} for *C. philander* and 3.4×10^{-4} for *L. pardalis*. The amount of simulated forest remnant restored was 11.4 million ha for *C. philander* and 12.6 million ha for *L. pardalis*, approximately 10% of the original extent of the Atlantic Forest. A 10.5% and 9.8% increase in habitat patch area resulted in a 5,518% (55-fold) and 4,100% (41-fold) increase in future habitat availability for *L. pardalis* and *C. philander*, respectively (Table 1).

Including targets for the habitat availability metrics provided the greatest increase in future habitat availability for both species (Table 1). These prioritizations tended to augment existing habitat patches making substantial contribution to current habitat availability (e.g. Araucaria sub-region). Only in one case was future habitat availability higher for the minimum cost strategy compared to any of the other strategies that included habitat availability metric targets (*DWA* for *C. philander*; Table 1). This can be explained because of a strong spatial autocorrelation in the land acquisition cost that resulted in restoration efforts creating a large block of contiguous forest, which has a pronounced effect on the future habitat availability. In all strategies the six biogeographical sub-regions achieved 20% of representation.

The costs of restoration varied from US$ 17.5 to 20.5 billion based on species and restoration strategy (Table 1). Minimum cost strategies were similar to strategies including targets for habitat availability metrics (US$ 19.7-20.5 billion for *L. pardalis* and US$ 17.5-17.6 billion for *C. philander*, respectively). As expected, the solution with the lowest costs was achieved by the minimum cost strategy (Table 1), because the increase in the number of targets constrains the solution.

The most cost-effective solution for both species were found when including targets for habitat availability metrics, specifically *sumΔPC* targets for *L. pardalis* and *DWA&sumΔPC* targets for *C. philander* (Table 1). These solutions broadly prioritized similar planning units for each species, with 75.6% and 80.8% of matching planning units for the *L. pardalis* and *C. philander* solutions, respectively (Fig. 3). These planning units were found mostly within Interior Forest and Araucaria sub-regions because these biogeographical sub-regions are cheaper and less degraded (so have high values for habitat availability metrics), respectively (Fig. 3). These areas cover 9.49 million ha given a land acquisition cost of US$ 14.1 billion.

(A) DISCUSSION

The problem this study addressed was how to prioritize land for restoration in an extensive and complex biome by incorporating the ecological value of habitat patch (habitat availability) into systematic conservation planning, while also considering biogeographical sub-region representation and cost-effectiveness. Our key findings are that 1) explicitly considering spatial configuration of habitat in restoration prioritizations resulted in substantial improvement to habitat availability; 2) these improvements were realized for minimal additional cost relative to solutions based solely on cost-minimization and biogeographical sub-region representation, and thus were cost-effective solutions; and 3) there was a high degree of concordance in priority areas for restoration for two species with widely different dispersal abilities and habitat patch requirements, suggesting such solutions may benefit a wide range of other species in the BAF. This study demonstrates the benefits of incorporating habitat availability measure into restoration prioritization problems.

The premise of our approach is that both the total amount of habitat and its spatial configuration are key drivers of metapopulation dynamics (e.g. Hanski & Ovaskainen, 2000; Fahrig, 2003; Visconti & Elkin, 2009) and species persistence (e.g. Santini *et al.*, 2014), but simple measures of aggregation or connectivity are unlikely to quantify habitat availability in an ecologically meaningful way (Saura & Pascual-Hortal, 2007; Noss *et al.*, 2009). However, quantifying habitat patch values using metapopulation models require that such models have been parameterized (often a difficult task) and that the number of patches is within reasonable computational limits (e.g. Westphal *et al.*, 2003). The BAF suffers in both of these regards: many of the species that inhabit the BAF are data deficient (Crouzeilles *et al.*, 2010), and the biome complexity renders formal metapopulation modelling infeasible. Instead, we identified two species with dispersal abilities and minimum habitat area requirements that may bracket a wide range of other species and used the *PC* metric, which is related to metapopulation models but easier to parameterize (Saura & Rubio, 2010; Appendix S1), to quantify habitat availability. We argue this approach strikes a reasonable balance between ecological relevance and computational pragmatism.

The high degree of concordance among selected planning units for the most cost-effective solutions for the two species provides some assurance that these prioritizations might benefit a wide variety of BAF mammal species. There are 298 mammal species within the BAF (Paglia *et al.*, 2012), dispersing between 20 m and 4,900 m based on a review for BAF species compiled by Crouzeilles *et al.* (2010). Data on dispersal is very scarce in the literature, but it is critical to estimate species-specific connectivity (Tischendorf & Fahrig, 2000; Crouzeilles *et al.*, 2013). Had we found little concordance among selected planning units it would have warranted finding data on dispersal ability and minimum habitat patch requirements for a wider range of mammal species, and then combining them into a single optimization framework.

Restoration involves different types of costs, thus cost-effective restoration priorities will vary according to the economic cost considered (Westphal *et al.*, 2007; Armsworth, 2014). Purchasing land for restoration is a current practice in the BAF. For example, since 2010 the company Symbiosis (www.symbiosisinvestimentos.com.br) has been purchasing land to restore with native plant species and sell timber products and carbon credits. We assumed that all land for restoration could be purchased at the current price (or the equivalent of current price given inflation) for each land-use in each county, because we lack finer scale spatial and temporal information on land acquisition cost. However, fluctuation in such values could influence our priorities, and future studies should account for uncertainty in future land prices.

Despite a large number of restoration projects worldwide, there is limited understanding of the costs of restoration (Holl & Howarth, 2000; Birch *et al.*, 2010). While land acquisition for restoration is a useful policy to be explored, restoration can involve other costs depending on the method used for restoration. For example, the cost of active restoration, involving seedling acquisition, replanting and monitoring for two years is estimated to be between US$ 49-77 billion to restore 15 million ha (*c.* US$ 3,315-5,216/ha; Calmon *et al.*, 2009). Thus, our predicted total land acquisition cost (between US$ 17.6-19.9 billion for the most-effective solution for each species) may not be the most expensive part of restoring the Atlantic Forest, unless restoration occurs passively (i.e. with no additional investment). Scientific recommendations regarding restoration costs and the development of economic mechanisms to facilitate restoration are critical for the Atlantic Forest Restoration Pact (Melo *et al.*, 2013). It may be unrealistic to restore 15 million ha of BAF through land acquisition, but the concordance of the most cost-effective solutions provided in this study identifies key areas where land acquisition may be appropriate and beneficial.

These overlapping priority areas for restoration are located mostly in the Interior Forest and Araucaria sub-regions. To date, only two studies have identified potentially suitable areas for restoration in the BAF (e.g. Calmon *et al.*, 2011; Tambosi *et al.*, 2014), one of the most endangered hotspots worldwide. First, members of the Atlantic Forest Restoration Pact mapped 18 million ha of illegally deforested land since 1965 according to Forest Code - the major Brazilian environmental law that protects forest on private lands (Calmon *et al.*, 2011). Most of these areas are also in Interior Forest and Araucaria sub-regions, but different locations are highlighted by Calmon *et al.* (2011). Tambosi *et al.* (2014) ranked landscapes for restoration considering the habitat amount and connectivity, identifying landscapes within Serra do Mar and Bahia sub-regions as restoration priorities. Thirty-three percent of the Serra do Mar sub-region remains standing, so we did not consider it a restoration priority at the BAF scale when considering the purchase of land as a mechanism to assist restoration. Our study contrasts with and complements both previous studies as they did not consider the associated costs of restoration, biogeographical sub-region representation, species with widely different ecological requirements and cost-effective analysis.

Theoretically it would have been possible to base our prioritization on the *PC* metric (habitat availability) directly, either using a simulated annealing algorithm or an exact method such as stochastic dynamic programming (Meir *et al.*, 2004; Westphal *et al.*, 2003). But such approaches are precluded by the computational cost of calculating *PC* (or other metapopulation measures) in complex systems such as the BAF. Our approach was to evaluate two habitat availability metrics (*PC* and *DWA*) that were related to metapopulation theory but that were only evaluated once, prior to optimization (current scenario), and then evaluate the solutions generated in the context of future habitat availability (*PC* calculated based on post-restoration simulated BAF). We demonstrate that this approach does yield substantial improvements in habitat availability in the solutions relative to solutions that based solely on cost-minimization and biogeographical sub-region representation.

Restoration is a global priority. Given limited budgets, restoration must be guided by information on their benefits and costs, maximizing return on investment (Rey Benayas *et al.*, 2009). To do this, novel spatial approaches need to be developed for restoration prioritization that consider many different socioeconomic and ecological values. Our restoration prioritization approach incorporates measures of metapopulation dynamics into systematic conservation planning, which could have profound implications for improving the value of restoration to many species.

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BIOSKETCH

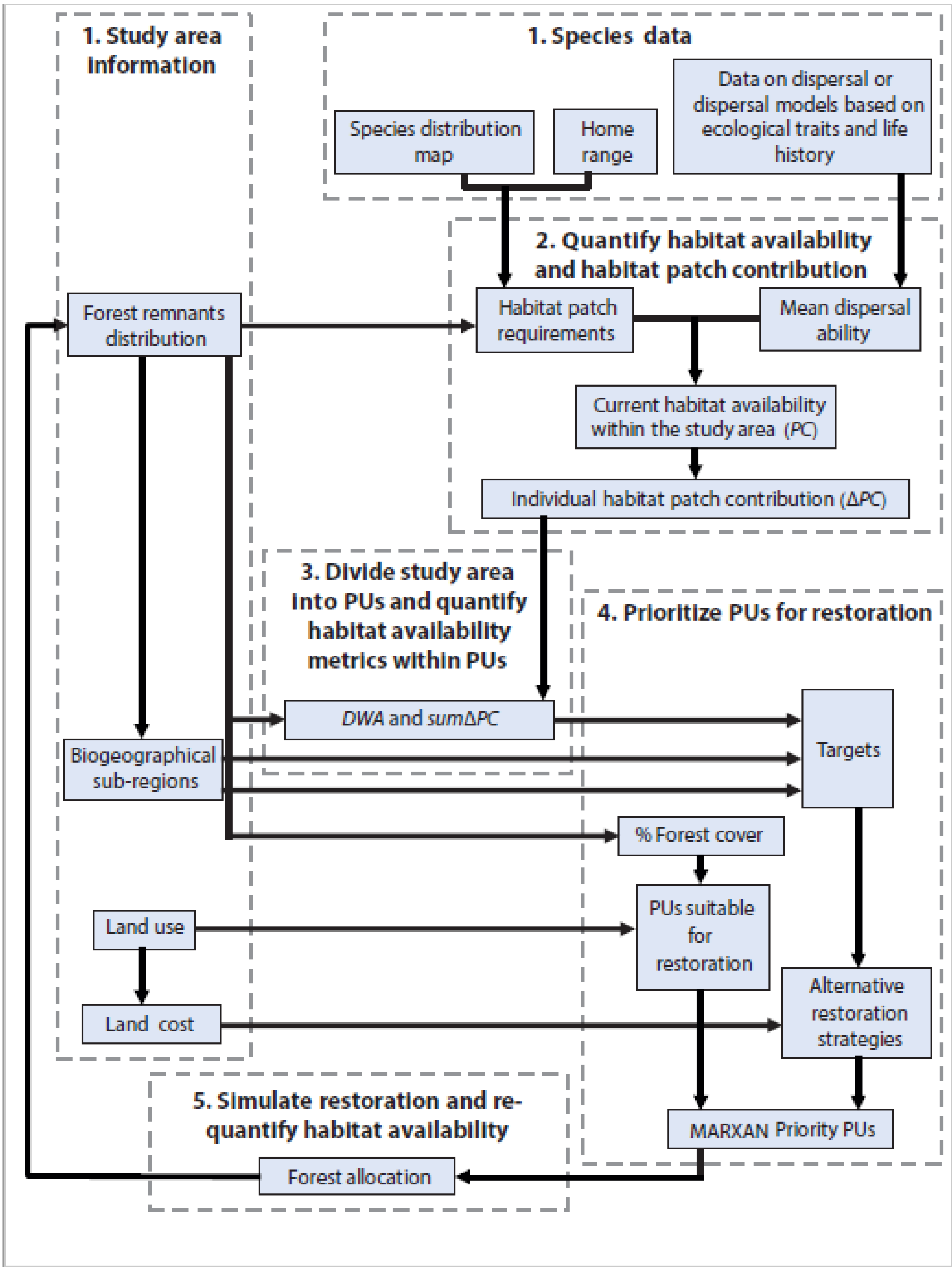
Renato Crouzeilles is interested in conciliating landscape ecology and restoration ecology to inform environmental management and public policies for conservation and restoration. In addition, he studies the effects of habitat reduction and fragmentation on biodiversity and ecological processes.

Author contributions: R.C. originally conceived the idea and H.L.B., M.M., C.E.V.G. and H.P.P. considerably improved on it; R.C. and H.L.B. built the database and a modified version of *Probability of Connectivity* index, R.C. and M.M. analyzed the data in Marxan. R.C. led the writing with considerable and substantial help from H.L.B. and M.M.

Table 1. Four alternative restoration prioritization strategies for each species. The first strategy did not consider habitat availability metrics, while the three other included targets for one of three habitat availability metrics. For each restoration strategy we calculated the improvement in habitat availability expressed as a percentage relative to current habitat availability, cost (billions US$) and cost-effectiveness based on the improvement in habitat availability divided by total land acquisition cost.

Restoration strategies	Improvement in habitat availability (%)	Cost (billion US$)	Cost-effectiveness
Caluromys philander			
Minimum cost	2,725	17.5	1.56
DWA	1,825	17.6	1.04
sumΔPC	3,075	17.6	1.75
DWA&sumΔPC	4,100	17.5	2.34
Leopardus pardalis			
Minimum cost	4,576	19.7	2.32
DWA	4,694	20.4	2.30
sumΔPC	5,518	19.9	2.77
DWA&sumΔPC	4,606	20.5	2.25

Figure captions



610 **Figure 1.** Restoration prioritization approach involves five main steps: 1) obtain data on study area and species; 2) quantify current habitat availability and the individual habitat patch contribution; 3) divide study area into planning units and quantify habitat availability metrics within each planning unit (sum of individual habitat patch contributions – *sumΔPC* and Distance-Weighted Area - *DWA*); 4) prioritize planning units for restoration; and 5) simulate restoration and re-quantify habitat availability. PUs – planning units.

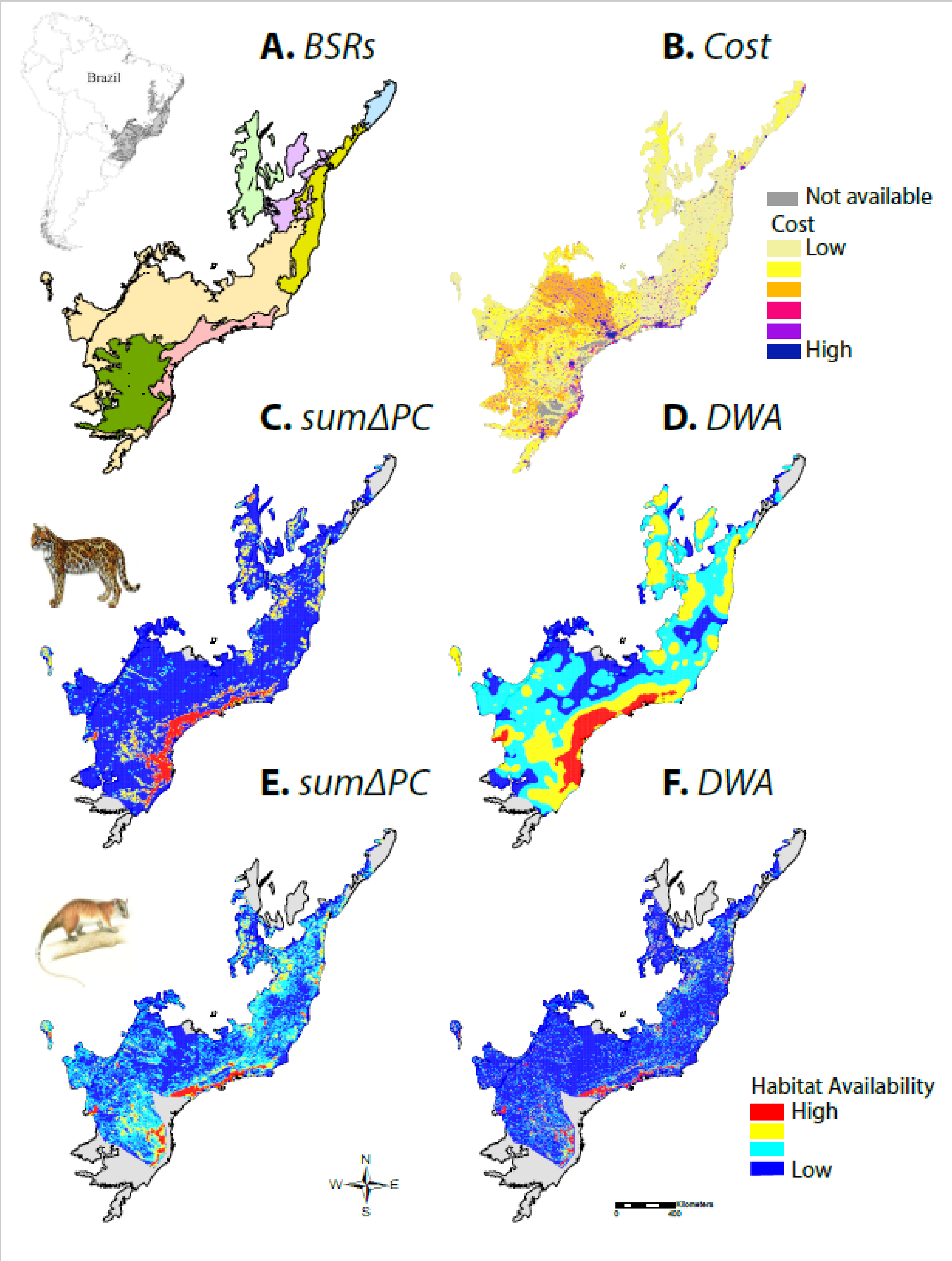


Figure 2. A) Biogeographical sub-regions of the Atlantic Forest: yellow – Bahia, pink – Serra do Mar, green light – São Francisco, green dark – Araucaria, blue – Pernambuco, purple – Diamantina and orange – Interior Forest. B) Land acquisition cost. Areas classified as "not
620 available" for restoration have >60% forest cover. Habitat availability for *Leopardus pardalis* based on C) *sumΔPC* and D) *DWA*. Habitat availability for *Caluromys philander* based on E) *sumΔPC* and F) *DWA*. Hottest colours represent planning units with higher contribution to the respective habitat availability metric. All values were classified using the geometrical interval method.

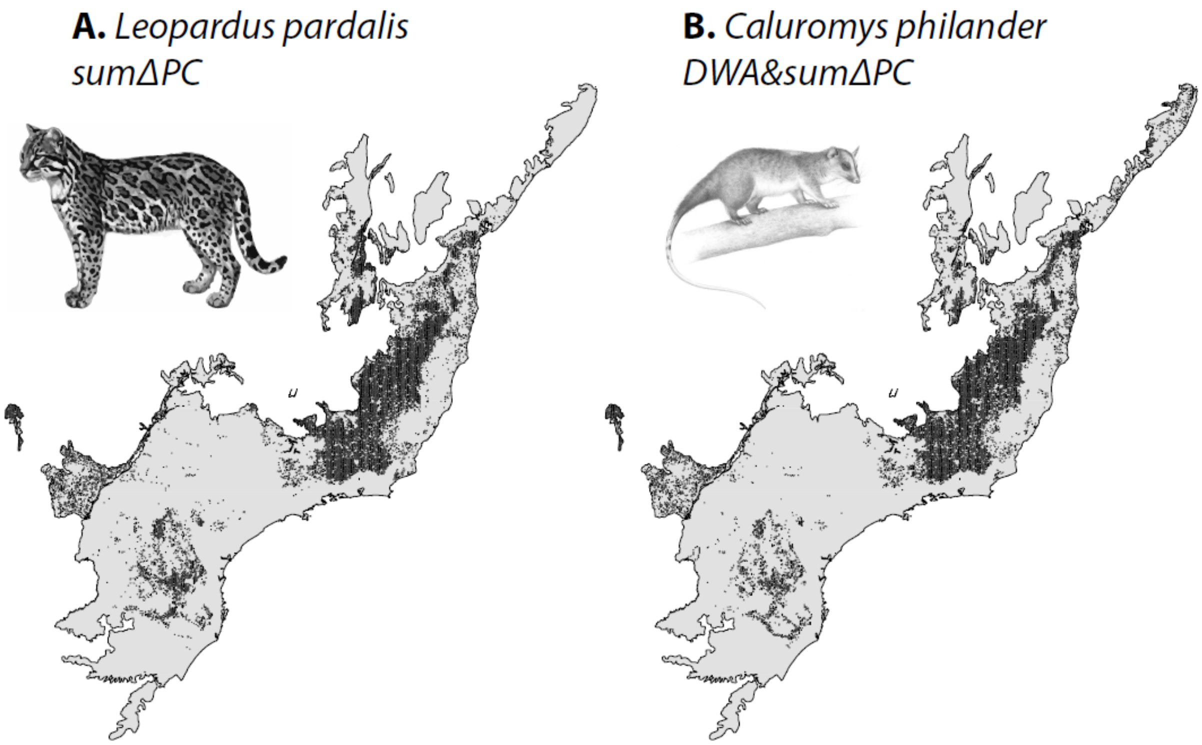


Figure 3. Simulated planning unit restoration for the most cost-effective strategy for: A) *Caluromys philander* and B) *Leopardus pardalis*.

Supporting Information

Appendix S1 – Quantifying metapopulation capacity and the relative value of patches in large networks

Probability of connectivity (*PC*) as a measure of metapopulation dynamics

The process of habitat loss and fragmentation can profoundly influence population dynamics through the combined effects of the: i) reduction in the total area of habitat available, ii) increased probability of local extinction in small patches, iii) reduced probability of dispersal between patches as the isolation distance exponentially increases, iv) increased number of patches at intermediate percentages of habitat and v) influence of this process on other aspects of ecological systems (e.g. predator abundance and distribution) (Andrén 1994; Fahrig, 2003; Crouzeilles *et al.*, 2014) .

Hanski & Ovaskainen (2000) develop "Metapopulation Capacity" (λ_M) as a measure of the capacity of a landscape to support a metapopulation. It is based on the Levins (1969) model in which the extinction and colonization dynamics of patches (i.e. patch occupancy) are related to patch area (or quality) and distance between patches. The extinction rate is inversely related to patch area, while the colonization rate is a function of the area of the patches from which dispersing individuals originate (e.g. larger patches generate more dispersers) and the distance to that patch (the probability of dispersal declines exponentially with increased distance).

λ_M is calculated as the leading eigenvalue of a population matrix (M) (Hanski & Ovaskainen, 2000):

$$m_{ij} = a_i\, a_j \exp(-\alpha d_{ij})$$

where a is the patch area, d_{ij} is the distance between patches i and j, and α is a species-specific parameter describing how dispersal probability declines as a function of distance. The values of the leading eigenvector of matrix M provide approximations of the relative contribution of each patch (λ_i) to λ_M (Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2003).

One benefit of this model is that only the patch areas, patch locations, and the species-specific dispersal parameter need be known. It can therefore be applied when patch-specific data on species densities and habitat qualities is not available. It also provides a global measure of system performance (λ_M) as well as local measures of the relative value of each patch (λ_i).

The cost of calculating the leading eigenvalue and its associated eigenvector for very large matrices is computationally problematic, and impractical for the Brazilian Atlantic Forest with more than 260,000 patches (consider that the size of matrix M is the number of patches squared). Saura & Rubio (2010) propose the "Probability of Connectivity" (*PC*) as an approximate measure of λ_M, and suggest that measures of the contribution of a patch to *PC* (*ΔPC*) can be quantified by removing a patch from the network and recalculating *PC* (the difference between the original and new *PC* value is the relative value of the patch). *PC* is calculated as (eq. 2 in main text):

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \, a_j \, p_{ij}^{*}}{A_L^2}$$

where a is the area of the patch, $p_{ij}*$ is the maximum product probability of all possible paths between i and j, and A_L^2 is a normalizing constant (e.g. the area of the landscape squared). The probability of connection between any two particular patches is $\exp(-\beta \, d_{ij})$ (eq. 1 in main text; note the similarity with the last part of m_{ij} above). The calculation of $p_{ij}*$ is a least-cost path network problem. Although this can be computationally expensive, it is feasible to calculate it exactly or approximately in large networks of patches (Appendix S2).

Here, we used 1000 simulated landscapes (a spatial domain between $0 \leq x \leq 100$ and $0 \leq y \leq 100$) to quantify the relationship between the overall landscape measures - λ_M and *PC*, and the patch-level measures – λ_i and *ΔPC*. We generated a variable number of patches (ranging from 10 to 200) as non-overlapping circles with radii ranging from 0.5 to 5 units within each simulated landscape (Fig. S1a). The distance units are arbitrary but could be thought of as km in this scenario. Euclidean distance was used to calculate the distance between the boundaries of the patches. Patch area was calculated as the area of the circles in measure. For each simulated landscape λ_M, *PC*, λ_i and *ΔPC* were calculated using α or $\beta = 0.05$. The simulations were implemented in R 2.12 (R Development Core Team, 2010).

PC is approximately linearly related to λ_M (Pearson's r 0.98; Fig. S1b) after standardizing *PC* to account for variation in the total area of habitat in the simulation (i.e. each estimate of *PC* was divided by the total area of habitat patches in the simulated landscape). *ΔPC* is approximately linearly related to $\sqrt{\lambda_i}$ (mean R^2 0.96 among all simulated landscapes; Fig. S2c, d).

Through simulation we establish that *PC* is a good approximation of Metapopulation Capacity (λ_M) and *ΔPC* is a good approximation of the relative value of each patch (λ_i). We conclude that *PC* and *ΔPC* are suitable alternatives to λ_M and λ_i for large problems in which it is infeasible or impractical to calculate the latter measures.

Appendix S2 – Details of our proposed methodological approach

Here, we provide further details regarding several aspects of our analysis (see Methods). Many of the species that inhabit the Brazilian Atlantic Forest are data deficient (Crouzeilles *et al.*, 2010), but dispersal ability information are required to estimate species-specific connectivity

(Tischendorf & Fahrig, 2000; Crouzeilles *et al.*, 2013). Thus, mean dispersal ability of *L. pardalis* was estimated from models considering ecological traits and life history of species (see for further details Whitmee & Orme, 2012).

The Brazilian Atlantic Forest is severely fragmented with more than 260,000 remnant forests and such number of patches computationally limits the calculation of the habitat availability metric used in this study (Probability of Connectivity index - *PC*). To overcome this limitation, we calculated a modified version of *PC* index. The original *PC* calculates p_{ij}^* among all pairs of patches (see step 2 in the Methods), but we calculated p_{ij}^* only between patches within a buffer distance representing the 99.9% probability of direct dispersal of species (eq. 1) performed around each habitat patch. We validated our modified version by comparing with original *PC* when calculated for smaller samples of the Brazilian Atlantic Forest. The Distance-Weighted Area metric (*DWA*) also suffered from the same problem found to calculate *PC* index in the Brazilian Atlantic Forest. For *DWA,* we only considered patches within a buffer of 99.9% of the probability of direct dispersal of that species (similar to modified *PC*), but in that case around a planning unit i (eq. 4).

To prioritize planning units for restoration, we used the conservation planning software Marxan (Ball & Possingham, 2000). The full Marxan objective function is given as follows:

minimize

$$\sum_{i=1}^{m} c_i x_i + b \sum_{i1=1}^{m} \sum_{i2=1}^{m} x_{i1}(1 - x_{i2}) cv_{i1,i2}$$

subject to the constraint that all the representation targets are met:

$$\sum_{i=1}^{m} a_{ij} x_i \geq t_j \forall j$$

where m is the total number of planning units, c_i is the cost of restoring planning unit i, x_i is the binary decision variable indicating whether planning unit i is selected ($x_i = 1$) or not ($x_i = 0$), and a_{ij} is the contribution of planning unit i to target j. The second component of the objective function, $b\sum_{i1=1}^{m}\sum_{i2=1}^{m} x_{i1}(1 - x_{i2})cv_{i1,i2}$, is the "boundary length modifier" (BLM) that controls the aggregation of planning units (Ball & Possingham, 2000). Specifically, $cv_{i1,i2}$ represents a penalty for selecting planning unit i but not selecting neighbouring planning unit j. The BLM was not used in this study, therefore our objective function simplifies to minimize $\sum_{i=1}^{m} c_i x_i$. We omitted BLM because *PC* evaluates connectivity and habitat configuration explicitly.

Marxan identifies priority planning units for restoration that meet the achievement of specific targets while minimizing cost. Targets are incorporated into the Marxan objective function within a "shortfall penalty function" that is based on the proportion of the target that is not met. The penalty only applies in cases where there is a shortfall (it is 0 otherwise). Expressing the shortfalls as proportions is a way of standardizing measures with different units (i.e. *sumΔ*PC, DWA, amount of biogeographical sub-region representation and amount of forest to be restored).

To build the forest cover and land acquisition cost maps we used land cover/land-use maps. Land-use maps were obtained from several sources: the Brazilian Ministry of the Environment (MMA, 2007), Ribeiro *et al.*, (2009), and the European Commission Joint Research Center (Eva *et al.*, 2000). The MMA map was primarily derived from TM/Landsat-5 images, at the scale of 1:250,000 (MMA, 2007). The Ribeiro *et al.*, (2009) maps were constructed from several other land-use maps with different spatial resolutions (see Ribeiro *et al.*, 2009 for details). The Vegetation Map of South America classifies 20 land cover classes of matrix within six broad classes, at a spatial resolution of 1 km, and based on four set of satellite data with different spatial resolutions (Eva *et al.*, 2000). The latter map was used only where coverage was absent from the other two maps.

We estimated land costs based on the 2012 yearbook of purchase prices of rural land. Specifically, we based acquisition costs on three general types of land use: pasture, agricultural land (agriculture and sugarcane) and livestock, stratified by county. Urban area land values were estimated using the Yearbook of the Brazilian Real Estate Market in 2011.

After identifying the priority planning units for restoration we simulated restoration of 60% forest cover within these selected planning units to quantify future habitat availability (post-restoration *PC*). The configuration of restored habitat within selected planning units was based on that of existing planning units containing between 59 to 61% of forest cover (n=128). We randomly rotated the habitat within existing planning units to increase the number of configuration possibilities before each allocation resulting in a total of 768 habitat configurations. The habitat within each selected planning unit was replaced with a randomly selected configuration from the set of 768, and *PC* was calculated based on this new configuration of habitat.

Finally, we estimate what land acquisition costs might be if they are not guided by an optimization procedure by randomly selecting planning units to meet the total area targets and the biogeographical representation targets. The cost of each of these solutions is then simply calculated as the sum of the cost of the randomly selected planning units. The minimum land acquisition cost that arose from 100 random restoration prioritizations was US$ 1.48 and 1.78 trillion for *C. philander* and *L. pardalis*, respectively, i.e. being 83- and 85.8-folds more expensive than all other strategies presented in the main text for each species.

Mathematical optimization provides pronounced cost savings relative to ad-hoc approaches to restoration prioritization. As an extreme example, random restoration prioritizations can be at least 83-folds more expensive than the solutions we identified. Clearly, there is enormous potential for efficiency savings by adopting a formal spatial prioritization approach. Indeed, the Brazilian government has recently re-affirmed its commitment to BAF restoration and is drafting a 20 year plan that includes the development of spatial prioritization strategies for restoration (MMA, 2015).

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Table S1. The biogeographical sub-regions (BSRs), current area (ha) and percentage of forest cover, and the minimum area required (ha) to be restored to achieve 20% of representation within each biogeographical sub-region (last line – total). The amounts required for restoration were based on the proportion of Brazilian Atlantic Forest covered by each species' range multiplied by the 15 million ha forest restoration target specified by the Atlantic Forest Restoration Pact.

BSRs	Area (ha)	% Forest cover	20% of representation (ha)	
			C. philander	*L. pardalis*
Serra do Mar	11,235,800	33		
São Francisco	10,655,400	9	780,564	1,221,170
Pernambuco	3,193,570	11	288,700	54,017
Araucária	24,468,500	14	984,113	1,354,389
Diamantina	8,211,920	13	385,800	553,740
Bahia	12,326,800	12	989,040	910,008
Interior Forest	66,611,700	7	8,033,787	8,471,771
Atlantic Forest	136,703,690	12	11,462,004	12,565,094

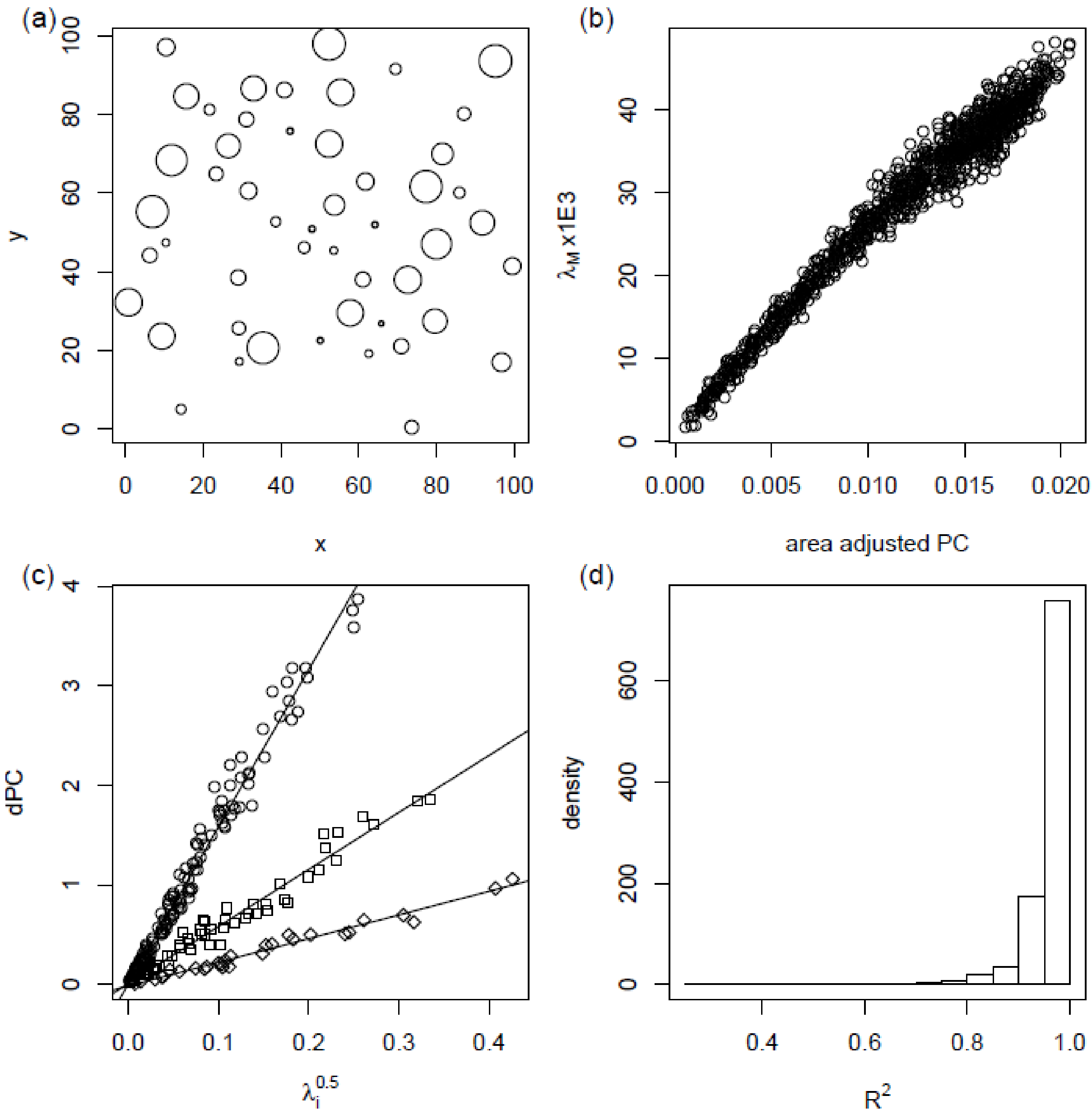

Figure S1. (a) Example of a simulated landscape with a random patch distribution. Circle radii are relative (patches are all non-overlapping). (b) The relationship between the overall landscape measures *PC* and λM quantified using 1000 simulated landscapes with variable numbers of patches (ranging from 10 to 200). (c) The relationship between the patch-level measures λ_i and ΔPC. For clarity only three representative examples are shown. The different slopes of the three examples are driven largely by different total amount of habitat areas in landscapes among simulations. Only the correlation of patch measures within a landscape is important. (d) A frequency distribution of correlations (R^2) between λ_i and ΔPC for all 1000 simulated landscapes.